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Research Article

Shell disease dynamics in the non-indigenous Atlantic rock crab (*Cancer irroratus*) in Icelandic waters

Sindri Gíslason[1], Hermann Dreki Guls[2], Joana Micael[1], Árni Kristmundsson[3], Mark Freeman[4], Nóa Sólrún Guðjónsdóttir[3], Halldór Pálmar Halldórsson[2]

1 *Southwest Iceland Nature Research Centre (SINRC), Garðvegur 1, 245 Suðurnesjabær, Iceland*
2 *The University of Iceland´s Research Centre in Suðurnes, University of Iceland, Garðvegur 1, 245 Suðurnesjabær, Iceland*
3 *Fish Disease Laboratory, Institute of Experimental Pathology, Keldur, University of Iceland, 112 Reykjavík, Iceland*
4 *Department of Biomedical Sciences, Ross University School of Veterinary Medicine, Basseterre, Saint Kitts and Nevis*

Corresponding author: Sindri Gíslason (sindri@natturustofa.is)

Abstract

Crustacean shell disease, characterized by progressive degradation of the chitinous exoskeleton due to secretion of chitinases and other enzymes by microorganisms, has been reported in crustaceans worldwide. Diseases affect all natural populations to some extent. However, under normal circumstances, they are generally not in high prevalence. Disease epidemics are regularly experienced in various marine animals. Data on their causes is often scarce, at least partly due to limited or nonexistent baseline data on the prevalence and intensity of even the most common agents, under normal circumstances. This study presents the first description of shell disease in the non-indigenous Atlantic rock crab *Cancer irroratus* in Icelandic waters, a finding of significant concern. Between June and August from 2017 to 2023, a total of 5,818 *C. irroratus* were sampled in Hvalfjörður, SW-Iceland. The shell disease was assessed in relation to sex, and the pattern of infection on exoskeleton surfaces was described. The prevalence and severity of shell disease showed a concerning upward trend, with the infection rate increasing from 47% in 2017 to 85% in 2023. Samples taken from diseased crabs and subjected to histological, bacteriological and molecular analyses, revealed severe bacterial infections in lesions, composed of a mix of nine species of chitinolytic bacteria of five genera. Furthermore, a known pathogenic oomycete (fungal-like organism) was observed in all crabs examined. As in similar crustacean shell disease studies, the condition in *C. irroratus* from Icelandic waters appears to result from synergistic effects of various bacterial species, possibly exacerbated by the observed oomycete pathogen. However, the cause of an epidemic like this is unknown and can only be speculated on with current knowledge.

Key words: *Cancer irroratus*, chitinolytic microorganisms, crustacea, Iceland, shell disease

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Introduction

Chitin is the second most abundant biopolymer in nature, preceded only by cellulose, functioning as the main structural component in various organisms, particularly crustaceans (Paulsen et al. 2016; Tsurkan et al. 2021). Chitinolytic microorganisms are, therefore, both common and vital to nutrient recycling (Keyhani and Roseman 1999). In crustaceans, the breakdown of chitin primarily occurs in the moulted shells, although not solely. The term shell disease refers to the progressive degradation of a crustacean´s exoskeleton, resulting from the secretion of chitinases and other enzymes

by a diverse community of microorganisms (King et al. 2014). Other names for these conditions include shell disease syndrome, 'classical' shell disease, black spot disease, rust spot disease, burnt spot disease, brown spot disease, bacterial shell disease, tail fan necrosis, and impoundment shell disease (Dyrynda 1998; Getchell 1989; Vogan et al. 2008; Shields 2013; Davies and Wootton 2018; Rowley and Coates 2023). According to Rowley and Coates (2023), not all these conditions share the same cause, with dysbiosis of different chitinolytic and lipolytic bacteria often implicated (Rosen 1967; Cipriani et al. 1980; Getchell 1989; Meres et al. 2012; Feinmann et al. 2017; Kraemer et al. 2020). Reports of cuticle abnormalities in crustaceans, collectively known as shell disease, date back to the early 20th century (Pearson 1908; Hess 1937). However, bacteria and decapod crustaceans have co-evolved for at least 160 million years (Robin et al. 2015a, b), with evidence of the earliest possible shell disease found in 100-million-year-old crab fossils (Klompmaker et al. 2016).

According to available literature, the disease typically starts with an erosion of the epicuticle, the non-chitinous outer layer of the exoskeleton. This damage is believed to arise from natural behaviors such as fighting (Sindermann et al. 1989), predation or cannibalism (Dyrynda 1998), and abrasion against sediment and hard surfaces (Young 1991; Vogan et al. 1999; Quinn et al. 2012) are believed to contribute to the onset of the disease by damaging the epicuticle. Additionally, various environmental stressors, including pollutants (Schlotfeldt 1972) and temperature fluctuations (Malloy 1978; Castro et al. 2006; Glenn and Pugh 2006; Tlusty and Metzler 2012), may increase crustacean susceptibility to shell disease. Once the underlying chitin-containing procuticle is exposed, shell degradation is largely attributed to the chitinolytic microorganisms (Getchell 1989; Stewart 1993). Although the disease is not believed to be fatal in its initial stages, mortality can occur later due to (i) unsuccessful moulting (e.g. Smolowitz et al. 1992) or (ii) septicemic infections caused by pathogenic microorganisms originating through the lesion sites (Baross and Tester 1978; Vogan et al. 2001). A vast variety of bacterial species of different genera can degrade chitin with chitinase (Brzezinska et al. 2014). Many different bacteria have been identified associated with exoskeletal lesions, and therefore all considered potential agents involved in this disease syndrome (Getchell 1989; Brzezinska et al. 2014). Furthermore, various chitin-degrading fungi and fungal-like organisms (e.g. oomycetes) are known, some of which are associated with diseases of crustaceans (Nakamura and Hatai 1995; Muraosa et al. 2012), but the factors triggering microbial invasion, proliferation, and degradation are still not fully understood.

The Atlantic rock crab *Cancer irroratus* Say, 1817 is one of the most recent members of the invasive alien species in Icelandic coastal waters, first reported in 2006 (Gíslason et al. 2014). Since then, the species has dispersed rapidly and is currently found clockwise from the southwest coast of Iceland to the east, corresponding to > 70% of the coastline (Gíslason et al. 2021). Its colonization may possibly be aided by the warming trend which began in the North Atlantic in 1996 and has led to noticeable changes in the Icelandic marine ecosystem (Anonymous 2004; Astthorsson and Palsson 2006; Astthorsson et al. 2007, 2012; Stefansdottir et al. 2010; Jochumsen et al. 2016). Increased shipping in recent decades has likely also contributed to the spread of *C. irroratus* since 2006 (Gíslason et al. 2021) and its success in Iceland is evident in its high abundance, reaching levels comparable to its native range in North America (Gíslason et al. 2017).

This study is critical since there is currently no information on shell disease in Icelandic waters. It provides baseline knowledge on the disease affecting *C. irroratus*

and may reveal connections to potential impacts on other shellfish species. Given the growing concern over the impact of non-indigenous species on native populations, identifying the various chitinolytic organisms, assessing their diversity, and understanding their pathogenicity is crucial.

This study aims to (i) evaluate the prevalence of shell disease among *C. irroratus* in Southwest Icelandic waters and (ii) identify infectious agents associated with the disease in Iceland.

Materials and methods

Sampling

Trap fishing was carried out in Hvalfjörður, SW-Iceland (Fig. 1). Hvalfjörður is about 35 km long and 3.5 km wide fjord, with maximum depth of 84 m. Sampling took place over 19 trips between June and August from 2017 to 2023. Each year, and during each sampling occasion, ten traps were deployed along a horizontal transect at five depth intervals (10, 20, 30, 40, and 60 m), with two traps at each depth interval. *C. irroratus* was captured using commercial crab traps (height 30 cm, length 80 cm, width 40 cm, mesh size 4.8 cm, with the escape opening for juveniles closed). Traps were baited with a mixture of fish, including gadoids (*Gadus morhua*, *Pollachius virens*, *Melanogrammus aeglefinus*). Mixed bait was placed in mesh bags hanging in the traps, ca. 500 g per trap. Baited traps remained in place for about 48 hours before retrieval. Captured crabs were identified by size and sex. Carapace width (CW) was measured to the nearest 0.1 cm between the two most distant points on the carapace, using a vernier caliper.

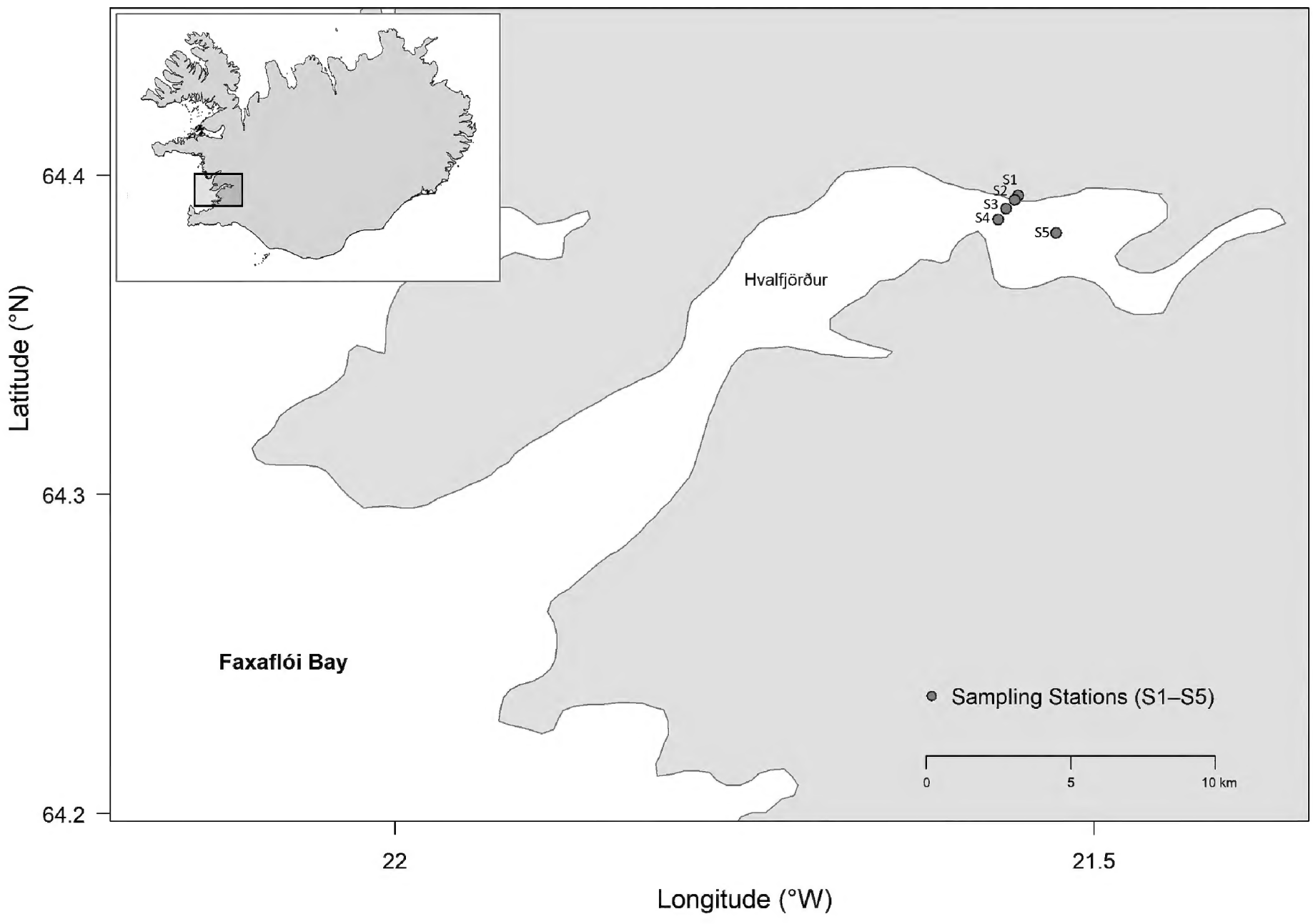

Figure 1. Location of the sampling stations in Hvalfjörður, SW-Iceland.

Shell disease assessment

The prevalence of shell disease in *C. irroratus* was monitored from 2017. Initially, the presence or absence of any visible shell lesions was recorded. In 2020, a graphical recording scale was implemented (Fig. 2) to better assess crab shell infections by identifying the specific locations on the crab exoskeleton (Fig. 3). This scale categorizes infection areas into four sections: 1) C = claws, 2) D = dorsal carapace, 3) E = carapace edge, and 4) L = legs. Visible signs of shell lesions were very rarely observed on the ventral carapace and therefore not included in the assessment.

Histology

A subset of six animals, caught in June 2021, were taken for histological examination. Tissues were excised from shell lesions and adjacent areas, fixed in Davidson´s fixative for 48 hours, and subsequently transferred to 70% ethanol. The samples were processed using standard histological protocols, i.e. decalcified, embedded in paraffin wax, sectioned, stained with Giemsa and mounted in resin-based medium. The histological slides were examined for pathogens and histopathological changes using a compound microscope.

Culture of bacteria

To get an idea of the pathogens associated with, and potentially causative agents of the lesions, samples from crabs (n = 6) were inoculated on two kinds of agar, i.e. blood agar with 1.5% NaCl (BAs), a general medium used for culturing

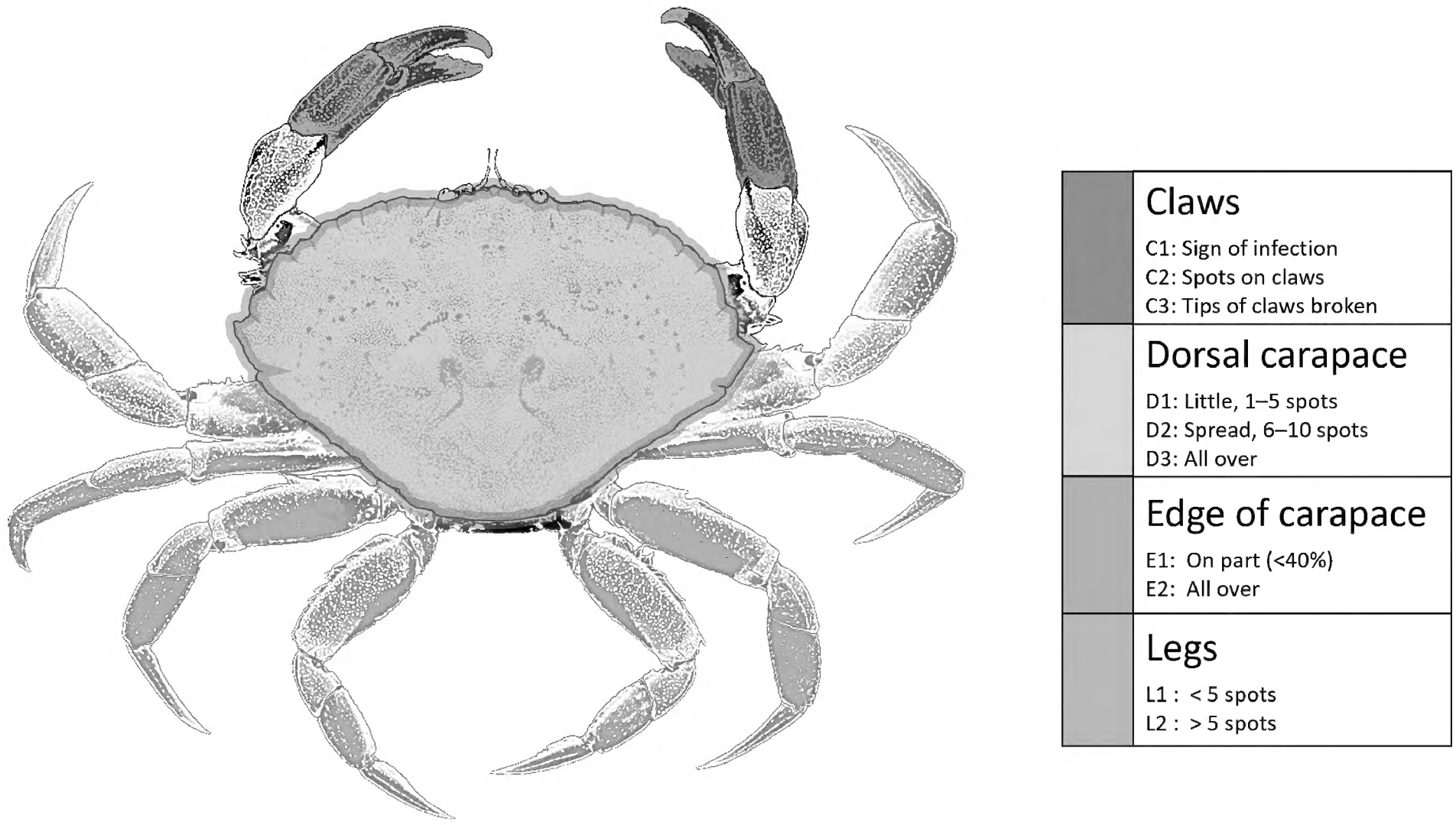

Figure 2. Shell disease was recorded in four areas on *Cancer irroratus* exoskeleton:1) claws, 2) dorsal carapace, 3) edge of the carapace, and 4) legs.

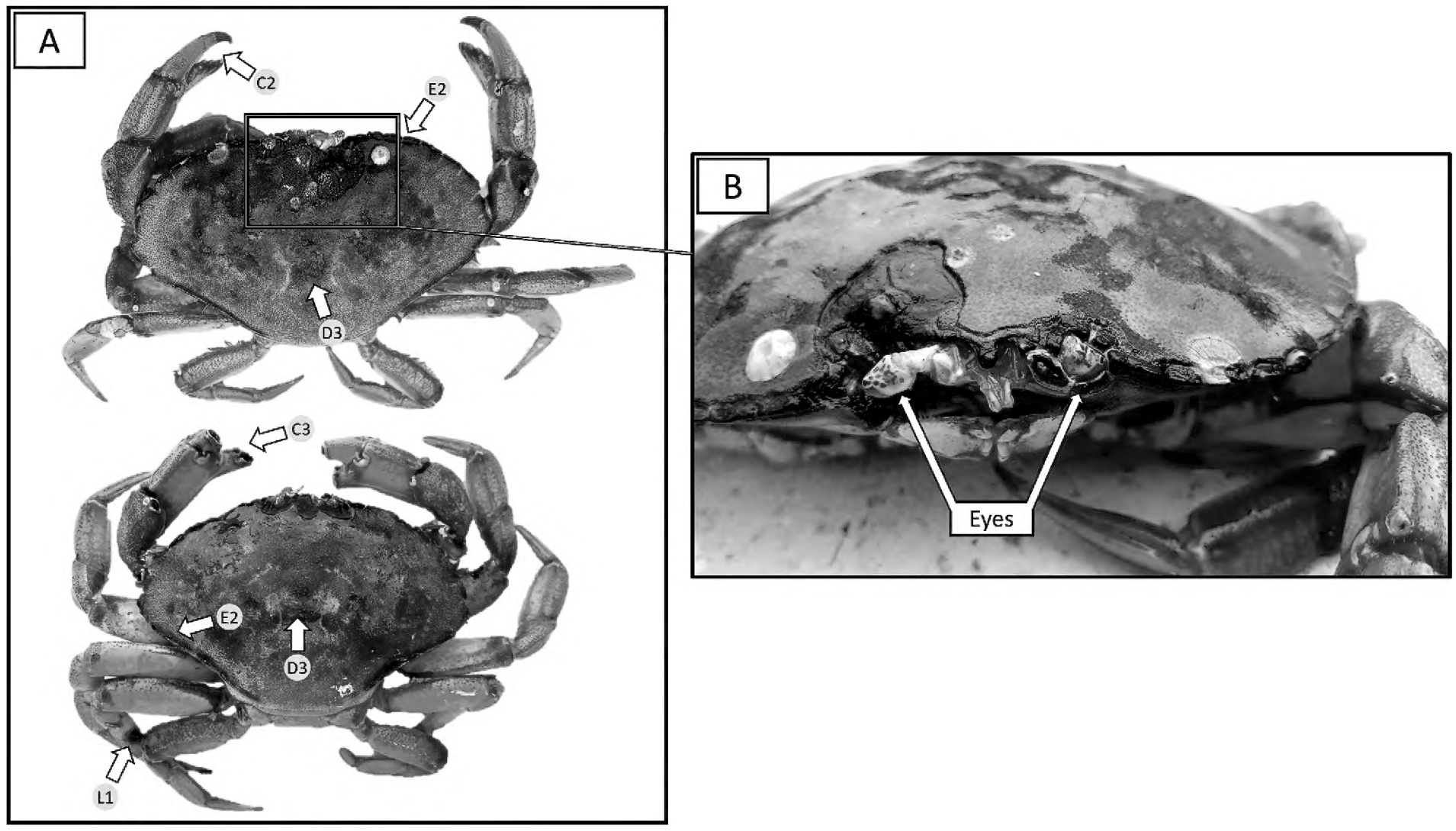

Figure 3. *Cancer irroratus* with shell disease. **A.** Distribution of lesions across the exoskeleton of two crabs, with arrows and numerical labels corresponding to the scale categories of infected areas shown in Fig. 2; **B.** Close-up of the anterior part of the carapace, showing intensive degradation of the crab's exoskeleton around the eyes. (Photos: Sindri Gíslason).

most common bacteria, and FMM (*Flexibacter maritimum* medium) a more selective medium used for culturing bacteria from the Family Flavobacteriaceae, a family of bacteria known to cause skin- and exoskeleton lesions in fish and crustaceans, respectively. Small pieces (approximately 4 mm^3) were excised from lesions, put in a mortel with 100 µl sterile seawater, and homogenized. A loopful of this homogenate, as well as from hemolymph, was inoculated on BAs but only from lesions on FMM blood agar with 1.5% NaCl. In addition to the original homogenate, three dilutions (10×, 100×, 1000×) were made and a loopful of those inoculated on the agar plates. This is a common procedure and done to avoid an overgrowth of faster-growing bacteria.

DNA isolation and sequencing

Bacteria

DNA was extracted from 32 bacterial isolates using GeneJet Genomic DNA purification kit (Thermo Fisher Scientific), according to the manufacturer's instructions. The 16S rRNA gene was amplified using the 8F and 1544R primers with 100–200 ng of template DNA and 0.8 µM final concentration of primers in a Veriti thermal cycler (Applied Biosystems). IllustraTM PuReTaq Ready-To-Go PCR beads (GE Healthcare) or Taq 2X Master Mix (New England BioLabs) were used for all PCR reactions in this study, in 25 µl reactions. The PCR conditions for amplification of the 16S rRNA gene were 95 °C for 5 min, followed by 35 cycles of 95 °C for 45 s, 55 °C for 45 s, 72 °C for 1 min and a final elongation

at 72 °C for 5 min. All primers in this study were from TAG Copenhagen. The PCR product was run on a 1% agarose gel (AppliChem), excised and purified using GeneJet Gel Extraction kit (Thermo Fisher Scientific). The 16S rRNA gene was sequenced by GeneWiz Europe using the 8F and 1544R primers. A nucleotide BLAST search (https://blast.ncbi.nlm.nih.gov/) was performed for each bacterial isolate to identify the closest known match.

Fungal-like organism

Tissue samples from crab lesions were put directly into a lysis buffer for genomic DNA extraction using a GeneMATRIX kit (EURx Poland) following the tissue protocol. Partial SSU rDNA (18s rDNA) from the fungal-like organism observed in histological sections was amplified from extracted DNA using the primer pair sfc-340f / sfc-1260r and PCR methods, designed to target a range of protist parasites (Kristmundsson et al. 2011; Kristmundsson and Freeman 2018). The PCR product was run on a 1% agarose gel, excised and purified using GeneJet Gel Extraction kit (Thermo Fisher Scientific). Sequencing reactions were performed using BigDyeTM Terminator Cycle Sequencing chemistry utilizing the same oligonucleotide primers that were used for the original PCRs. DNA sequencing was performed in both forward and reverse directions for all PCR products, and nucleotide BLAST searches were performed for each sequence to confirm a non-host/parasite origin. The contiguous sequences were obtained manually using CLUSTAL_X and BioEdit (Hall 1999).

Statistical analysis

Linear regression analysis was used to assess changes in size (carapace width) over time for all *C. irroratus* sampled, both overall and by sex. Fisher's exact test (Fisher 1934) was used to compare sex-based differences in shell disease prevalence across individual years and over the full study period.

To evaluate the effects of depth, sex, and size (carapace width) on shell disease prevalence, binomial logistic regression models were fitted separately for each predictor (Hosmer and Lemeshow 2000). Depth was modelled as a categorical variable with 10 m as the reference depth. For size, separate models were fitted to improve interpretability. Regression coefficients were exponentiated to yield odds ratios (OR), and model precision was evaluated using 95% confidence intervals (CI) and p-values calculated using Wald tests (Wald 1943).

Model performance was assessed using four complementary metrics. The Akaike Information Criterion (AIC) was used to assess model parsimony (Akaike 1974). McFadden's pseudo-R^2 (McFadden 1974) and Tjur's R^2 (Tjur 2009) were used to evaluate explanatory power. Discriminative ability was evaluated using the area under the receiver operating characteristic curve (AUC) (Hanley and McNeil 1982). Model assumptions were considered appropriate based on visual inspection and lack of convergence warnings. Multicollinearity was not a concern due to the use of single-predictor models.

All statistical analyses were conducted in R version 4.3.3 (R Development Core Team 2024). Data visualizations were created using the ggplot2 package (Wickham 2016).

Results

Trap fishing

A total of 5,818 *C. irroratus* specimens were caught between June and August from 2017 to 2023 (Table 1, Suppl. material 1: fig. S2). This species accounted for more than 99% of the total catch. Two other crab species were caught in the traps, *Carcinus maenas* (Linnaeus 1758) and *Hyas araneus* (Linnaeus 1758), but in far fewer numbers or only 70 and 37 individuals in total, respectively. Due to the low abundance of these native species, shell disease was not investigated in these crabs.

In total, 4,480 male and 1,138 female *C. irroratus* were caught. Males outnumbered females in all trap catches, with their proportion ranging from 62 to 94% (Table 1). The mean size of males was 12.1 cm (range: 6.7 to 15.1 cm), and 8.8 cm for females (range: 6.1 to 10.5 cm). A statistically significant increase in male carapace width ($p < 0.001$) was observed over the study period. No significant temporal trend in carapace width was observed for females ($p = 0.61$) (Fig. 4).

Shell disease in *Cancer irroratus*

The documentation of shell disease in *C. irroratus* in Iceland started in 2017, with 47% of the captured crabs infected (Table 2). Since then, the disease has steadily increased, and in 2023, the prevalence of infected crabs was 85%.

Prevalence by depth

Logistic regression revealed that shell disease prevalence in *C. irroratus* increased significantly with depth (Fig. 5). Compared to 10 m, the odds of disease were 1.18 times higher at 20 m (95% CI: 1.04–1.38, $p = 0.014$), 2.19 times higher at 30 m (95% CI: 1.88–2.56, $p < 0.001$), 3.50 times higher at 40 m (95% CI: 2.89–4.27, $p < 0.001$), and 2.04 times higher at 60 m (95% CI: 1.72–2.42, $p < 0.001$) (Suppl. material 1: table S1). Model performance metrics included AIC = 7571.17, AUC = 0.615, McFadden's $R^2 = 0.032$, and Tjur's $R^2 = 0.041$ (Suppl. material 1: table S2). No evidence of multicollinearity or poor model fit was detected in residual diagnostics. These results indicate that the likelihood of disease roughly doubles or triples at mid-to-deep depths relative to shallow areas. Notably, while the proportion of the disease at 40 and 60 m depth was already high at the beginning of the study (82% and 56% in 2017, respectively), it further increased to 88% and 79% in 2023.

Table 1. Total catch of *Cancer irroratus* in Hvalfjörður per year, month, and sex (M = male, F = female).

Year	Total		June		July		August	
	M	F	M	F	M	F	M	F
2017	370	44	103	24	121	8	146	12
2018	364	154	105	2	153	67	106	85
2019	491	226	135	61	201	70	155	95
2020	1105	243	308	22	356	159	441	62
2021	725	32	344	17	-	-	381	15
2022	622	155	-	-	246	105	376	50
2023	803	484	289	57	209	271	305	156

(-) Not measured.

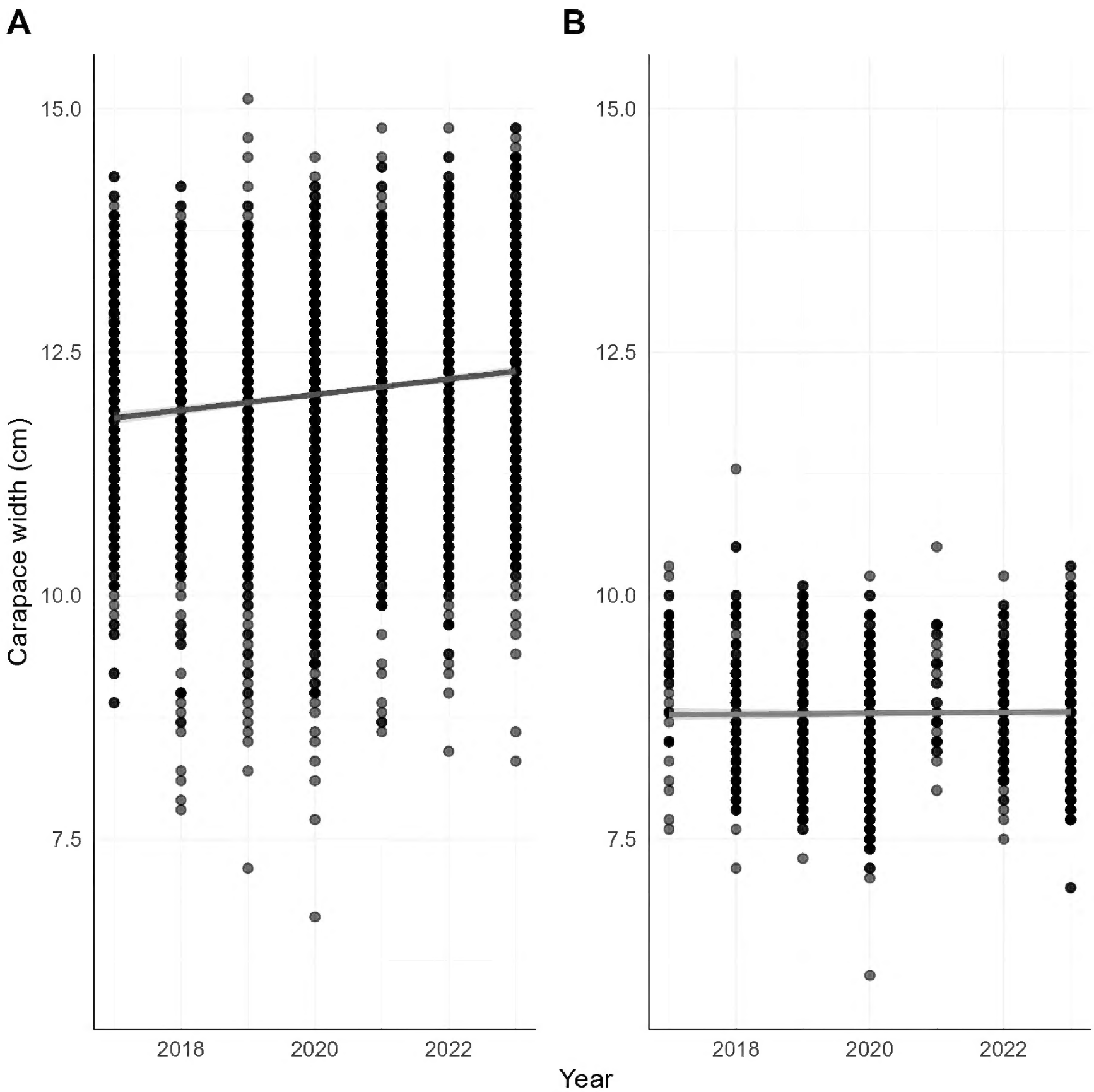

Figure 4. Scatter plots with linear regression lines showing the trends in carapace width of *Cancer irroratus* in Hvalfjörður, SW-Iceland, from 2017 to 2023. Each individual crab is represented by a gray dot, with the dot darkening as the density of crabs behind each dot increases. (A) Males exhibit a significant positive trend in carapace width over time, whereas (B) females do not show a statistically significant change in carapace width throughout the study period.

Table 2. *Cancer irroratus* caught in traps in Hvalfjörður per year shown by the total number of individuals, number of crabs with shell disease, and the distribution of shell disease across different body parts (C: claws, D: dorsal carapace, E: edge of the carapace, L: legs) and intensity of infection (1–3) according to the scale shown in Fig. 2.

Year	Total	Total	%	C			D			E		L	
	captured	infected	infected	C1	C2	C3	D1	D2	D3	E1	E2	L1	L2
2017	414	196	47	-	-	-	-	-	-	-	-	-	-
2018	518	262	51	-	-	-	-	-	-	-	-	-	-
2019	717	327	46	-	-	-	-	-	-	-	-	-	-
2020	1348	846	63	48	271	290	252	261	156	452	190	27	23
2021	757	471	62	11	81	255	88	104	174	225	147	41	37
2022	777	545	70	22	63	192	131	132	179	293	145	49	14
2023	1287	1089	85	44	62	296	147	204	242	289	306	99	31

(-) Not measured.

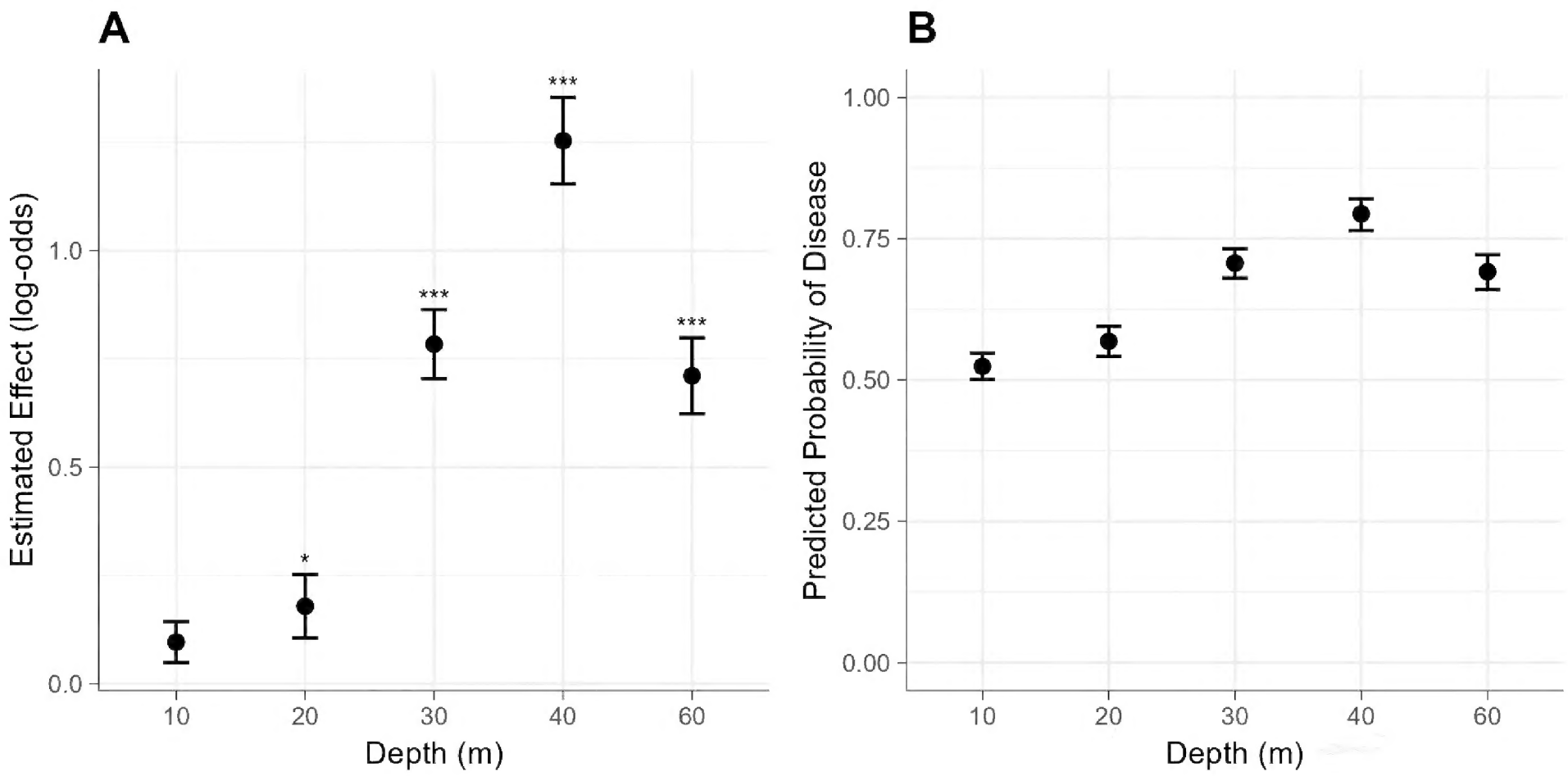

Figure 5. Logistic regression analysis showing the relationship between depth and shell disease prevalence in *Cancer irroratus* in Hvalfjörður, Iceland (2017–2023). **A.** Regression coefficients (log-odds) for each sampling depth, with 10 m as the reference category. Asterisks indicate statistical significance: ***$p < 0.001$, *$p < 0.05$; **B.** Predicted probabilities of shell disease occurrence at each depth based on the fitted logistic regression model. In both figures, error bars represent 95% confidence intervals.

In contrast, prevalence at 10, 20, and 30 m began lower but steadily rose throughout the study period. By 2023, disease prevalence at these shallower depths reached levels comparable to, or in some cases exceeding, those previously observed at 40 and 60 m (Suppl. material 1: fig. S1). These findings indicate that although deeper waters initially had higher disease prevalence, the increasing rates at shallower depths over time suggest a dynamic interaction between depth and temporal factors in shaping shell disease emergence and progression.

Prevalence by sex

Over the entire study period, shell disease was more prevalent in females (76.8%) than in males (60.4%). This difference was statistically significant (Fisher's Exact Test, $p < 0.001$). Logistic regression supported this result, showing that females had 2.16 times higher odds of infection than males (OR = 2.16, 95% CI: 1.88–2.49, $p < 0.001$). Model performance metrics for the sex model were as follows: AIC = 7475.10, AUC = 0.674, McFadden's $R^2 = 0.036$, and Tjur's $R^2 = 0.021$.

When analysed by year, highly statistically significant differences between males and females were observed in 2019, 2020, 2022 and 2023 ($p < 0.001$ for each year), while no significant differences were found in 2017 ($p = 0.43$), 2018 ($p = 0.44$) and 2021 ($p = 0.19$).

Prevalence by size

Logistic regression models revealed a positive association between size and shell disease prevalence in both sexes. For males, each 1 cm increase in carapace width was associated with an 18% increase in the odds of disease (OR = 1.18, 95% CI:

1.14–1.28, p < 0.001). For females, the odds increased by 42% per cm (OR = 1.42, 95% CI: 1.13–1.78, p = 0.0023) (Suppl. material 1: table S1).

Model performance was stronger for the size models than for other predictors. For males, AIC = 5979.00, AUC = 0.722, McFadden's R^2 = 0.054, and Tjur's R^2 = 0.009. For females, AIC = 1445.54, AUC = 0.693, McFadden's R^2 = 0.042, and Tjur's R^2 = 0.008.

These results are also reflected in the predicted probability curves (Fig. 6), which show a clear upward trend in disease likelihood with increasing carapace width for both sexes, based on sex-specific logistic regression models.

Infected areas on shells

The distribution of shell disease lesions on *C. irroratus* exhibited significant temporal shifts over the study period. Kruskal-Wallis was used to test for each area to compare the intensity of black spots over the years. Post-hoc comparison was then performed to compare the intensity of black spots for each body part (claws, back, carapace edges,

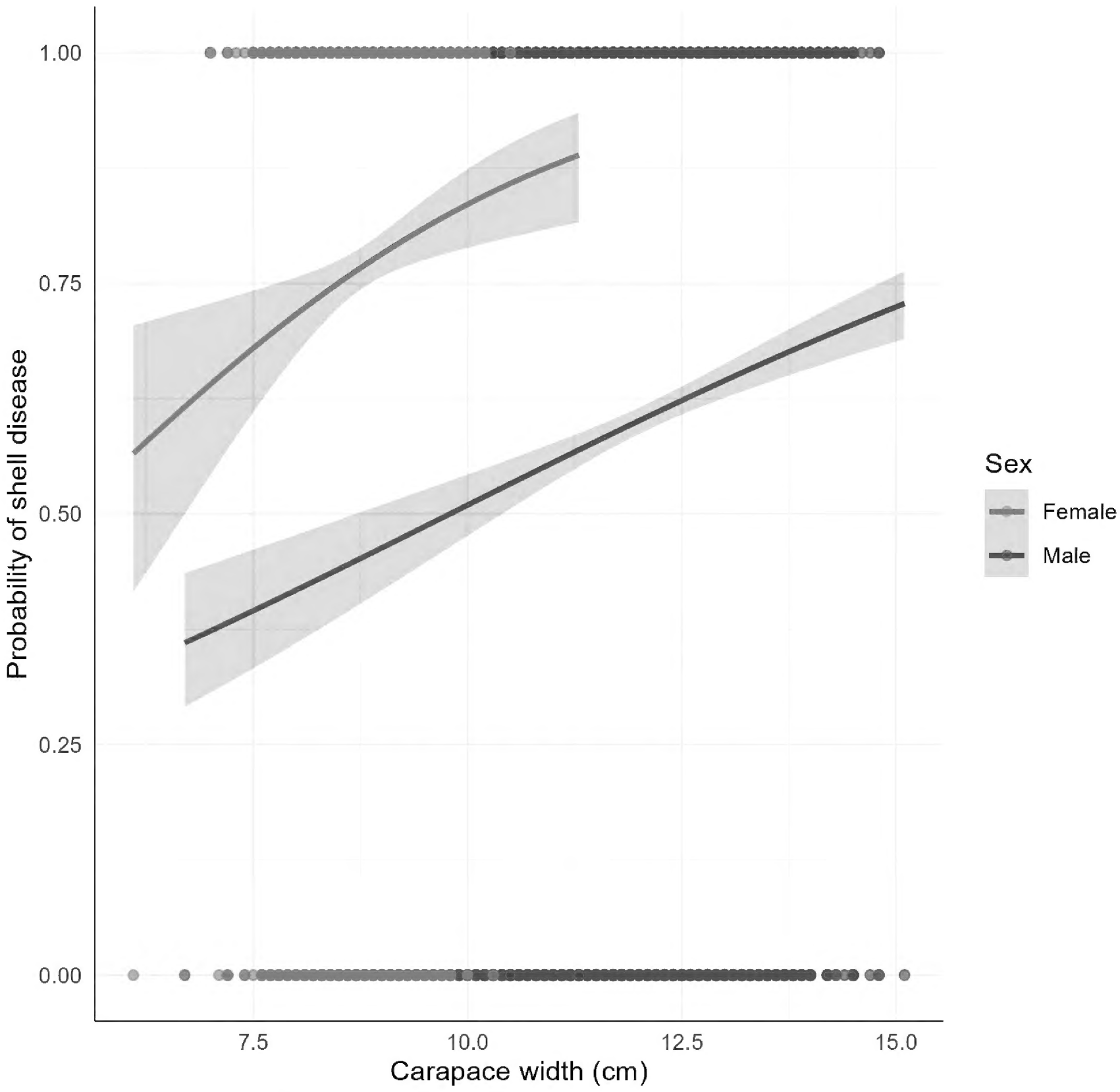

Figure 6. Predicted probability of shell disease in *Cancer irroratus* by size (carapace width), based on sex-specific logistic regression models for males and females. Shaded areas represent 95% confidence intervals.

legs) across different years (2020 to 2023). The p-values were then adjusted using the Bonferroni method to account for multiple comparisons. Infections in legs decreased significantly between the years 2020 and 2023 ($p < 0.001$), while the intensity of shell disease in the claws, dorsal part- and edges of the carapace increased significantly ($p < 0.001$ in all cases) (Fig. 7). These findings highlight a statistically significant temporal shift in the distribution of black spot disease across different body areas of the species, possibly influenced by environmental or biological factors that vary from year to year.

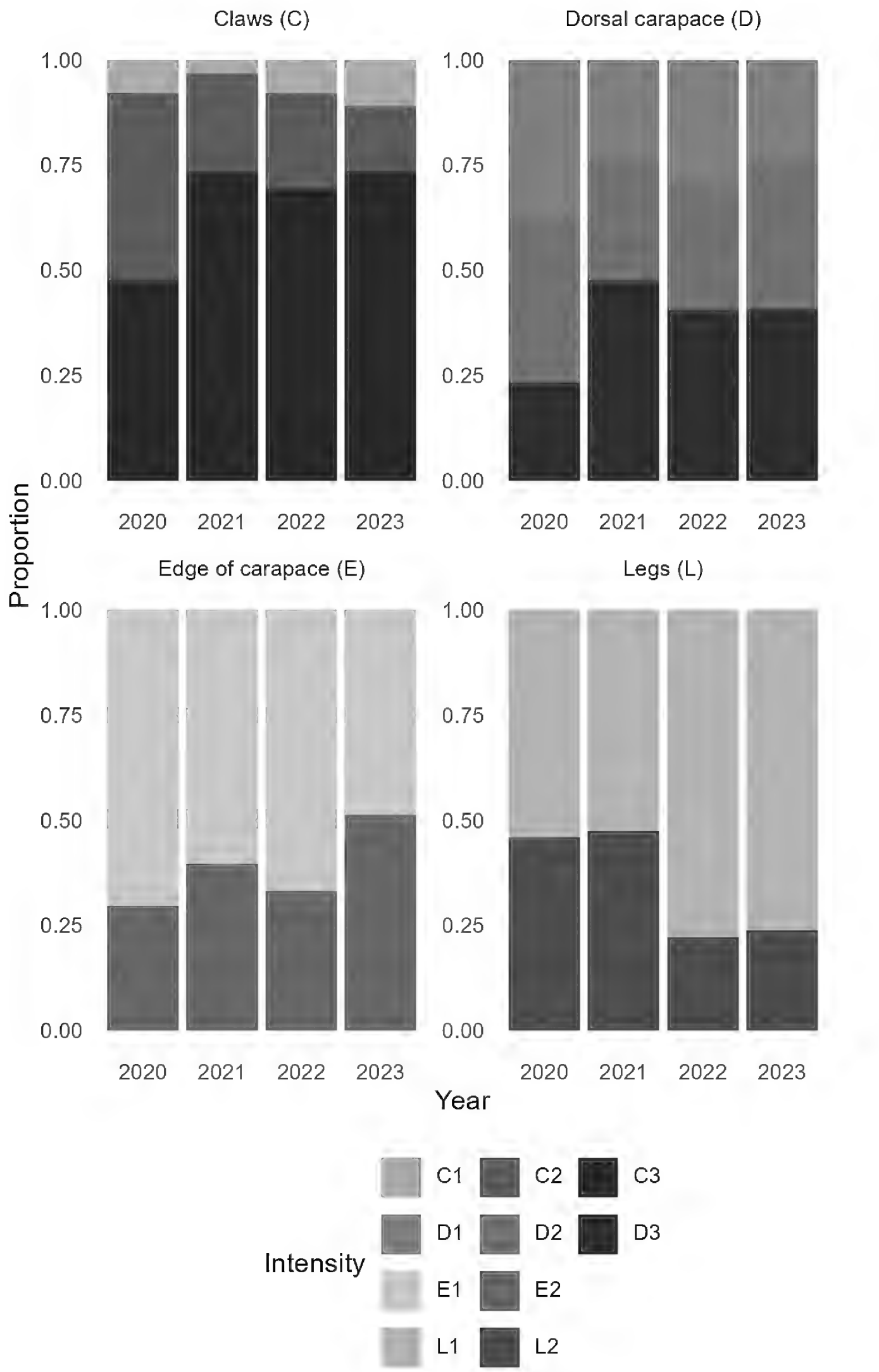

Figure 7. Intensity of shell disease in *Cancer irroratus* is shown proportionally by affected areas by year, according to the recording scale (see Fig. 2). Darker colours represent increased intensity of shell disease.

Histopathology

A varying degree of histopathological damage was observed in the exoskeletons of all examined crabs. Focal light necrosis was observed in both the exo- and endocuticle, with initiating bacterial proliferation, even in apparently healthy crabs with a seemingly normal epicuticle (Fig. 8A, B). With further progression of the disease, the epicuticle became eroded/necrotized, leading to more widespread necrosis and bacterial proliferation in the exocuticle, as well as melanization of the epi- and exocuticle, while the endocuticle remained only lightly affected (Fig. 8C, D). In the most severe cases, widespread severe necrosis of all cuticular layers was observed, associated with high abundance of rod-shaped bacteria (Fig. 8E, F).

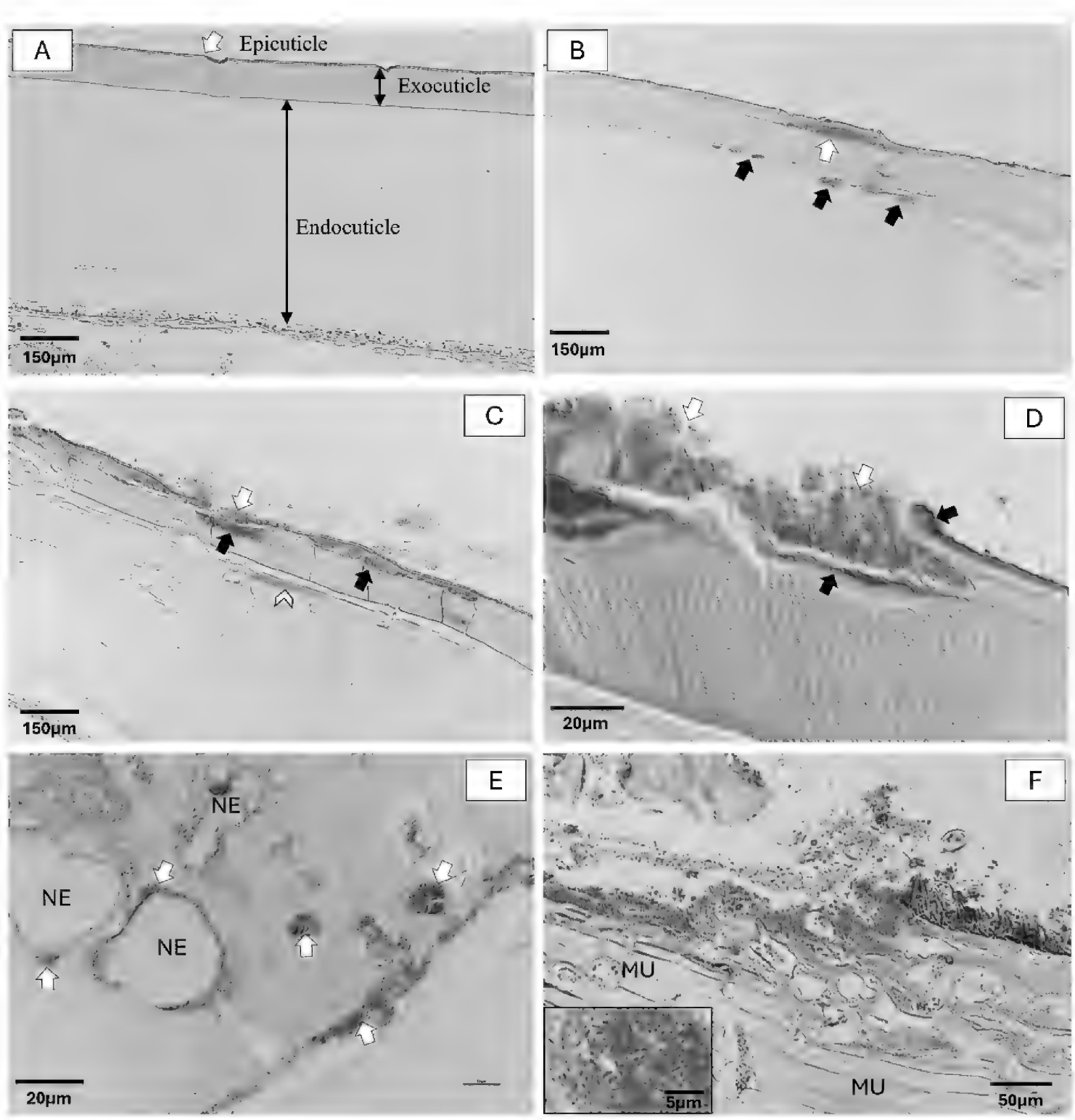

Figure 8. Histological observation of shell disease in *Cancer irroratus* from Hvalfjörður, SW-Iceland. **A.** Normal structure of the exoskeleton of *C. irroratus*, showing the outermost non-chitinous epicuticle and the underlying chitin-containing exo- and endocuticle; **B.** An apparent initiation of bacterial infection, showing clusters of bacteria under a seemingly undamaged epicuticle, extending into the exocuticle (white arrows). Additional colonizations of bacteria are evident at the boundaries of the exo- and endocuticle (black arrows); **C.** More advanced infection with focally eroded/necrotized epicuticle (white arrow), and further bacterial proliferation, especially in the exocuticle (black arrows), but still the endocuticle is only lightly affected (arrowhead); **D.** Higher magnification of bacterial infection in the epi- and exocuticle (white arrows), with obvious melanization in both layers (black arrows); **E.** With further progress of the infection, the epi- and exocuticular layers are absent and massive proliferation of bacteria are evident in the endocuticle (white arrows). Note the necrotic areas within the endocuticle (NE) caused by the chitinolytic activity of the bacteria; **F.** Complete necrosis of all layers of the exoskeleton, associated with high abundance of bacteria, extends somewhat into the underlying muscular layer (MU). Inset: Bacteria at higher magnification.

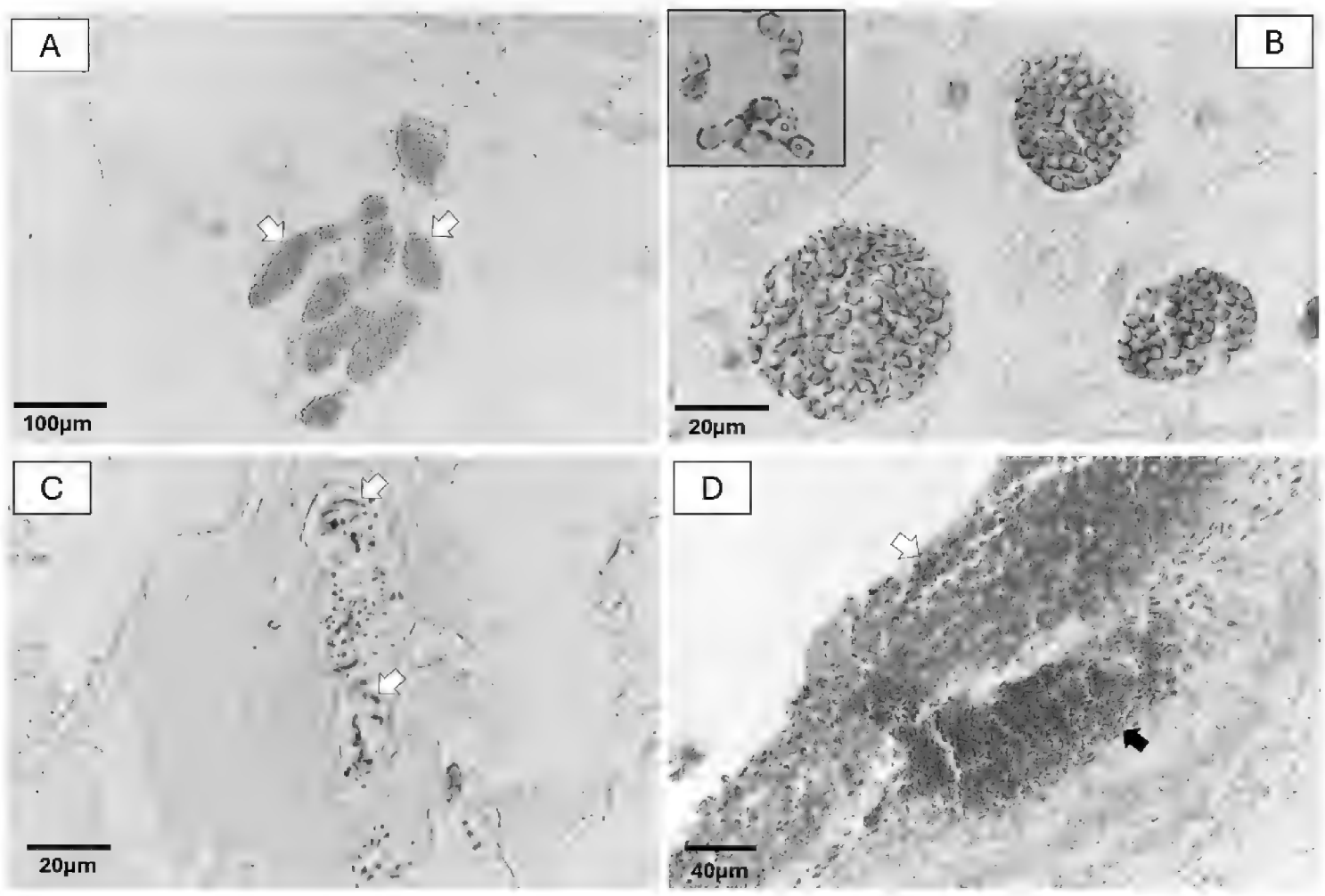

Figure 9. Fungal like organisms (oomycete) detected in diseased *Cancer irroratus* from Hvalfjörður, SW-Iceland. **A.** Cluster of presumable zoosporangia in the vicinity of the exoskeleton; **B.** Higher magnification of zoosporangia, showing 2–3 µm sized zoospores (inset); **C.** Fungal-like hyphae within a necrotized area of the endocuticle (arrows); **D.** Masses of bacteria (white arrow) and free zoospores (black arrow) in an area where the cuticle is completely necrotic and absent.

Bacterial infections were mainly restricted to the cuticle but commonly extended somewhat into underlying tissue. In addition to bacteria, fungal-like forms were observed in all crabs, the most common form detected being 25–100 µm oval to elongated zoosporangia, enclosing numerous circular/oval zoospores, measuring 2–3 µm (Fig. 9A, B). In some cases, clusters of free zoospores and hyphae-like forms were detected among the bacteria. Like the bacteria, the fungal-like forms were associated with lesions (Fig. 9C, D). However, they were also widespread within other tissues. Melanization of the cuticle layers was common in the larger lesions, an immune response of the crab to injury and/or microbial infections.

Infectious agents isolated from lesions

Bacterial culture gave 32 isolates, 24 from lesions and eight from haemolymph. The PCR product performed on these isolates revealed nine bacterial species of six genera from lesions and haemolymph. Of those, three *Vibrio* spp., two *Psychrobacter* spp. and one species of each of the genera *Photobacterium*, *Pseudoalteromonas*, *Pseudomonas* and *Aliivibrio* were detected (Table 3). Four of the species observed were isolated from both lesions and haemolymph, suggesting a systemic infection, while five species were isolated only from the crab lesions (Table 4).

In search of the fungal-like organisms observed in histological sections, PCRs done on samples from lesions resulted in successful amplification of the unknown parasite. All PCR products of the expected size were bidirectionally sequenced using the same primers, and a consensus sequence of 823 bp was constructed. A BLAST search of the databases revealed a 99.2% similarity to *Atkinsiella dubia* [AB284575], a pathogenic marine Oomycete (Peronosporomycetes), that was isolated from the eggs from the Asian blue crab, *Portunus trituberculatus*,

Table 3. Bacteria species isolated from *Cancer irroratus* in Hvalfjörður, SW–Iceland, showing the highest similarity to known Genbank sequences and assigned GenBank accession numbers of the isolates.

Species of bacteria	Present study		Highest GenBank similarity (Accession number)	No. of isolates sequenced
	Accession number	Length (bp).		
Vibrio gallaecicus	PV612259	1423	99.14% (KR270248.1)	6
Vibrio splendidus	PV612260	1415	99.50% (EU091336.1	8
Vibrio tapetis	PV612261	1406	99.93% (HE795151.1)	2
Aliivibrio logei	PV612262	744	99.87% (JQ361740.1)	1
Pseudoalteromonas porphyrae	PV612263	1416	99.93% (AY771715.1)	4
Photobacterium frigidiphilum	PV612264	1429	99.79% (NR_042964.1)	3
Psychrobacter alimentarius	PV612265	1411	100% (CP014945.1)	1
Psychrobacter fjordensis	PV612266	1391	99.64% (NR_148330.1)	4
Pseudomonas fulva	PV612267	1414	99.86% (AB681094.1)	3

Table 4. Summary of bacteria presence in six specimens of *Cancer irroratus* from Hvalfjörður, SW–Iceland. [a] Isolated from FMM agar only.

Species of bacteria	Proportion of infected crabs	No. of isolates from lesions	No. of isolates from haemolymph
Vibrio gallaecicus	6/6	5	1
Vibrio splendidus	4/6	5	3
Pseudoalteromonas porphyrae	4/6	3	1
Photobacterium frigidiphilum	3/6	1	2
Vibrio tapetis	2/6	2	-
Aliivibrio logei	1/6	-	1
Psychrobacter alimentarius	1/6	1[a]	-
Psychrobacter fjordensis	4/6	4[a]	-
Pseudomonas fulva	1/6	3[a]	-

from Japan. The sequences generated in this study were identical across all sampled crabs. The consensus sequences were submitted to GenBank and assigned the accession number PV627786.

Discussion

The prevalence of shell disease in *C. irroratus* in Hvalfjörður, SW-Iceland, has reached an alarming 85%. Typically, shell disease occurs at much lower frequencies in natural populations (Sindermann et al. 1989), making this finding particularly concerning. This discrepancy raises significant concerns about the health and sustainability of the local crab populations.

Shell disease in *C. irroratus* is not unprecedented and has been reported within its native range since the 1970s (Young and Pearce 1975; Sindermann et al. 1989; Sawyer 1991). Background rate in its native habitat has been reported to be less than 5%, with significantly higher prevalence in contaminated areas i.e. around 20% (Sawyer 1991). The drastic increase in disease rates within the Icelandic population requires a comprehensive investigation of contributing factors and potential management strategies. This rapid increase in shell disease prevalence is particularly concerning given the non-native status of *C. irroratus* in Iceland. Since its introduction around the year 2000, it has thrived well in its northernmost Atlantic Ocean habitat (Gíslason et al. 2014), expanding its distribution to cover over 70% of Iceland´s coastline (Gíslason et al. 2021). While annual monitoring at fixed transects since 2007 (Gíslason et al. 2021) has previously recorded occasional instances of melanization on damaged exoskeletons, the significant shift to

widespread shell disease prevalence, particularly noticeable since 2017, highlights the rapid change in the health status of the Icelandic population of *C. irroratus*. This major change called for documentation of the disease that started in 2017, and already at that time the prevalence was 47% of the population. Since then, the trend of the disease has worsened and affected 85% of the population in 2023. Reports of high prevalence of shell disease in crustaceans are rare, especially where it exceeds 50% of the population. However, similar high prevalence rates have been reported in other crustacean species, including *Chionoecetes tanneri* (Baross et al. 1978), *Callinectes sapidus* (Sandifer and Eldridge 1974; Rogers et al. 2015), *Cancer pagurus* (Vogan et al. 1999) and *Homarus americanus* (Groner et al. 2018).

This highlights the need to better understand the factors contributing to the spread of this disease, particularly in the context of non-indigenous species. Our study revealed that size, sex and depth are key factors that appear to influence the prevalence of shell disease in *C. irroratus*.

Shell disease prevalence increased significantly with size. This relationship with size has previously been noted for *C. irroratus* (Sawyer 1991), and several other crustacean species (Ayres and Edwards 1982; Nottage 1982; Sindermann et al. 1989; Young 1989; Sainte-Marie and Dufour 1994; Dyrynda 1998; Vogan et al. 1999; Castro and Angell 2000; Cobb and Castro 2006; Castro et al. 2012; King et al. 2014; Davies et al. 2015). The frequency of moulting varies significantly among species, sexes, and size classes (Vogt 2012) and smaller individuals tend to moult more frequently, indicating a longer intermoult phase as they age, a pattern observed in other species like *C. pagurus* (Bennett 1974), *Neohelice granulata* (Luppi et al. 2004), *Paralithodes camtschaticus* (Nilssen and Sundet 2006), and *Halicarcinus planatus* (Diez and Lovrich 2013). This suggests that the higher occurrence of disease in larger slower-growing individuals, including reproductive females, could result in moulting frequency being too low to rid the organism of early infection (Glenn and Pugh 2006). Juvenile *C. irroratus* usually moult at least once a year (Reilly and Saila 1978). For *C. irroratus* in Iceland, moulting intervals for individuals with carapace width larger than 7 cm range from one to three years (Gíslason et al. 2017), suggesting a lifespan much longer than previously reported for the species in its native range (Reilly and Saila 1978). This prolonged intermolt phase with age is likely to have significant effects on the prevalence of shell disease in Iceland as it allows more time for potential penetration of the non-chitinous epicuticle. The majority of newly moulted *C. irroratus* in our study were free of clinical signs of shell disease, whereas terminally moulted crabs showed a higher prevalence of the infection as they do not shed the infected carapace. This variation in intermoult periods for larger *C. irroratus* in Iceland (Gíslason et al. 2017) is likely due to genetic differences, which may also contribute to physiological variations between geographic regions (Darling et al. 2008; Tepolt et al. 2009).

Sex

We observed a skewed sex ratio, with 77% of individuals caught being males. This aligns well with previous observations on *C. irroratus*, attributed to sex-specific behaviour (Gíslason et al. 2021). An examination of the prevalence of shell disease across sex and sizes revealed clear patterns. The highest prevalence levels were found in larger crabs, particularly larger females, with females showing significantly higher prevalence of shell disease in most years. A similar trend has been

noted in *Homarus americanus*, where ovigerous females show higher indices of shell disease than both males and non-reproductive females due to delayed moulting cycles (Castro et al. 2012; Howell 2012), contrary to most species, where males are generally more affected by the disease (Sandifer and Eldridge 1974; King et al. 2014), as they live more aggressive lifestyles that may lead to injuries exposing the exoskeletal chitin (Sindermann et al. 1989; Vogan et al. 1999). The burrowing behaviour of *C. irroratus* is also likely to be a contributing factor. Burrowing has been suggested to cause abrasions and subsequent increases in lesions in other species, e.g. *C. pagurus* (Vogan et al. 1999). It is known that chitinolytic bacteria are most abundant in the upper layers of mud (Zobell and Rittenberg 1938), making bottom-dwelling species that burrow into bottom sediments more prone to infection. These bacteria are unevenly distributed due to the patchy distribution of nutrient particles and their colonization tendencies (Zobell and Anderson 1936). The highest concentrations of chitinolytic bacteria are found in coarser sediments such as sand, where chitinous particles accumulate (Zobell and Rittenberg 1938). In the topmost mud layers, there can be up to a thousand chitinolytic bacteria per gram, but their numbers decrease sharply with depth, though some can still be found in mud cores over 60 cm deep. *C. irroratus* is highly adapted to live on flat and fine substrate bottoms. The species exhibits exceptional sustained locomotion abilities and can quickly disappear beneath the sand, burying itself up to its eyes within seconds (Jeffries 1966). This behaviour is likely to result in sediment abrasion injuries when buried. To our knowledge, no sex-related difference in burrowing behaviour, such as time spent in the sediment or burrowing technique, has been documented. However, slight sexual dimorphism (Bigford 1979), with mature females having longer carapace and deeper bodies than males of equivalent length (Shotton 1973), could contribute to differences in abrasion susceptibility.

Depth

Our findings demonstrated a statistically significant positive correlation between depth and shell disease, with the highest prevalence at 40 m. Based on our data (Suppl. material 1: fig. S2) the number of crabs per trap does not indicate that field density (estimated by trap catches) at different depths influences the prevalence or severity of shell disease. Notably, the highest catches per trap occurred at 10 and 20 m where the prevalence of shell disease was the lowest throughout the study period, indicating that factors other than density, such as depth-related environmental conditions, might be more influential. To our knowledge, this increase in shell disease with depth has not previously been documented in comparative studies on crustaceans (Comely and Ansell 1989), although variations in prevalence at different depths have been observed for some species, such as *Homarus americanus* (Tanaka et al. 2017). As discussed earlier, female *C. irroratus* in Hvalfjörður showed a higher relative frequency of shell disease across all depths compared to males, suggesting sex-specific factors contributing to the observed depth-related differences in disease prevalence. However, these findings should be interpreted cautiously, as other factors, such as salinity and temperature, might be influencing the presence of the disease (Tanaka et al. 2017). For instance, shell disease is strongly linked to water temperature and tends to be most severe in the warmest months (Rogers et al. 2015). This correlation can be explained by the fact that pathogens causing shell disease, such as *Vibrio* spp. and other bacteria, are more prevalent at higher temperatures (Huq et al. 1984; Welsh and Sizemore 1985).

Predictive ability of size, sex, and depth

Although depth, sex, and size were all statistically significant predictors of shell disease, model performance metrics indicate that these variables alone explain only a portion of the observed variability. Discriminative ability ranged from modest (AUC = 0.615 for depth) to fair (AUC = 0.722 for size in males), while pseudo-R^2 values remained low across all models. This is consistent with findings from other ecological studies involving multifactorial diseases and large, imbalanced datasets (Hammert 2016). These results suggest that additional factors such as environmental stressors, microbial load, molting frequency, or host condition may play important roles in shell disease dynamics.

Infectious agents associated with lesions

Abnormalities in cuticle of crustaceans, collectively termed shell disease, date back to the 1930s (Hess 1937; Rowley and Coates 2023). According to Rowley and Coates (2023), not all these diseases share the same pathology or etiology, and three main forms of have been defined. Type 1 is characterized by progressive erosion of the cuticle, and caused by changes in structure of the bacterial community (Castro et al. 2012; Shields 2012; Vogan et al. 2008; Bergen et al. 2022), Type 2 is characterized by melanization reactions on the surface of the cuticle, but with minor or no cuticular erosion, believed to be caused by penetration of the cuticle by fungi and/or oomycetes (Makkonen et al. 2013; Yao et al. 2022; Rowley and Coates 2023). Type 3 represents a condition of unknown etiology, possibly linked with metal pollutants. Changes in pigmentation occur, but no erosion of the cuticle (Andersen et al. 2000; Dennis et al. 2016). According to this definition, it seems that the epidemic in *C. irroratus* in Icelandic waters is a mix of Types 1 and 2, i.e. severe erosion of the cuticle, associated with melanization and significant bacterial and oomycete infections.

Since the beginning of research on shell diseases of crustaceans, a great variation of pathogens have been reported as potential causative agents of this condition. Most of those are a vast variety of bacterial species, but also fungi and fungal-like organisms (e.g. Makkonen et al. 2013; Rowley and Coates 2023). Commonly, many different species of bacteria are isolated in each study and from the same individual, which suggests that the disease is caused by the synergistic effects of many different pathogens. It therefore seems difficult to pinpoint any particular species of bacteria or pathogens as a primary cause for shell diseases. To date, the causes of shell diseases in crustaceans are thought to be caused by a complex of microorganisms (Bell et al. 2012; Chistoserdov et al. 2012; Meres et al. 2012; Rowley and Coates 2023), a result of dysbiosis, i.e. an imbalance in the microbiome of an individual, often leading to disease of different chitinolytic and lipolytic bacteria (Rosen 1967; Cipriani et al. 1980; Getchell 1989; Meres et al. 2012; Feinmann et al. 2017; Kraemer et al. 2020). An unusual form of shell disease, termed 'white leg disease', which affects larval stages of lobster species in cultivation in Australia, seems to be an exception to the generally accepted 'polymicrobial view'. Traditional culture and NGS, suggests that this disease is caused by a single species of bacteria, i.e. *Aquimarina* sp., and apparently independent of other pathogens (Ooi et al. 2020; Rowley and Coates 2023).

In the present study, only six crabs from one-time point (June, 2021) were examined for infectious agents. As noted above, the bacterial flora associated with shell diseases generally differs significantly between studies. Consequently, the data presented

is very limited, and the pathogens observed cannot be looked at as representatives for the whole epidemic, but rather an idea of potential causative agents of the disease. Nine different species of chitinolytic bacteria, representing six genera, i.e. *Vibrio*, *Pseudoalteromonas*, *Photobacterium*, *Aliivibrio*, *Psychrobacter* and *Pseudomonas*, were identified in diseased *C. irroratus*. Species of all these genera have been found to be associated with shell diseases of crustaceans in previous studies (Getchell 1989; Vogan et al. 2002; Costa-Ramos and Rowley 2004). Five of the species of bacteria were identified in more than one crab, one from all six (*Vibrio gallaecicus*) and two from 4/6 individuals (*V. splendidus* and *Pseudoalteromonas porphyrae*). Furthermore, five species, *V. gallaecicus*, *V. splendidus*, *P. porphyrae* and *Photobacterium frigidiphilum*, were isolated from both lesions and hemolymph. That might indicate that infections by these bacteria were septicemic/systemic in the crabs, and that they are potentially causing pathology in inner organs, as well as the exoskeleton. Being chitinolytic, it seems highly possible that the intestinal tract of the crabs could be affected, as large parts of it are lined with a cuticle (Štrus et al. 2019). Furthermore, infections being systemic, it is not unlikely that the formation of lesions is not exclusively via penetration of the exoskeleton but could actually initiate from inside of the animal. Indications of that were observed in histological examination, where bacterial proliferation and necrosis were present at sites where the epicuticle seemed normal.

A number of true fungi and oomycete species (Peronosporomycetes) have been shown to be pathogenic to crustaceans (Makkonen et al. 2013; Yao et al. 2022; Rowley and Coates 2023), *Aphanomyces astaci*, the causative agent of crayfish disease is without much doubt the best-documented oomycete species affecting crustaceans (e.g. Svoboda et al. 2017). Another example is the fungi *Fusarium avenaceum* (Ascomycota), which causes ´burn spot disease syndrome´ in the nobal crayfish *Astacus astacus* (Makkonen et al. 2013). Data on *Atkinsiella dubia*, identified from all the diseased crabs, is limited. It has, however, been reported as a significant pathogen of the Japanese mitten crab (*Portunus trituberculatus*) and Asian blue crab (*Eriocheir japonicus*) from Japanese waters (Nakamura and Hatai 1995; Roza and Hatai 1999). The possible contribution of *A. dubia* to the shell disease in Icelandic waters remains unclear. However, based on its apparent pathogenicity in other crab species, it should be considered as a potential pathogen of other crab species, with a possible role in the shell disease in *C. irroratus*.

Shell disease may be transmissible under certain conditions, particularly in communal seawater systems (Fisher et al. 1978; Sindermann et al. 1989). High population densities in marine reserves can exacerbate the prevalence of shell disease (McCallum et al. 2005; Wootton et al. 2012; Wood et al. 2013) due to increased competition, stress and frequent interactions among conspecifics (Debuse et al. 2003; Wootton et al. 2012), facilitating disease transmission (Vogan et al. 1999; Whitten et al. 2014). Thus, the mechanisms by which high population densities enhance disease spread include: 1) increased competition for resources such as habitat and food, resulting in stress; 2) higher pathogen release into the environment; 3) and greater likelihood of encounters between hosts and pathogens (Castro et al. 2012). As populations grow, so do interactions between individuals, which can cause injury and disease (Davies et al. 2015). This all fits well with what we are seeing in Iceland, as a recent publication by Gíslason et al. (2021) on *C. irroratus* in Iceland shows that the population of the non-indigenous species is still in the growth phase. It also shows that the species is currently the most abundant brachyuran crab species on soft-bottom habitats in Southwest Iceland (Gíslason et al. 2021) and found in densities that

are among the highest reported for the species in its native range (Gíslason et al. 2017). The high prevalence of shell disease observed in *C. irroratus* in Iceland raises significant concerns about its future impact on this species and potentially native crustacean populations. Diseases are known to alter community composition, age distributions, and trophic interactions (Harvell et al. 2002), which underscores the potential ecological implications for Icelandic ecosystems. This is particularly alarming as it marks the first time chitinolytic bacteria have been documented in Icelandic waters, and the severity and prevalence of the disease are notable. Marine infectious disease outbreaks have historically caused widespread mass mortalities, yet the lack of baseline data has hindered the evaluation of whether these diseases are increasing or decreasing (Tracy et al. 2019). Iceland is no exception in lacking such baseline data. Indeed, available data from long-term monitoring of native commercial species, such as *Nephrops norvegicus* since 1950 and *Pandalus borealis* since 1960, show no reports of shell disease (Eiríksson and Jónasson 2018; Jónsdóttir et al. 2017). Similarly, studies on *Hyas araneus* for potential commercial exploitation did not report any sign of shell disease (Einarsson 1988). The recent detection of shell disease in Iceland, and its global recognition for impacting commercial fisheries by increasing mortality rates and reducing market value (Sindermann et al. 1989; Messick and Sindermann 1992; Vogan 2008; Tanaka et al. 2017; Jithendran et al. 2024), might be coincidental. It is possible that the bacteria are native to Icelandic ecosystems and that native species have developed resistance. Alternatively, these pathogens might have been introduced through shipping, possibly with *C. irroratus* from North America. If that is the case, the population decline in the native species *Carcinus maenas* and *Hyas araneus*, in the study area reported by Gíslason et al. (2021), could be linked to the pathogens. From that point of view, it should be noted that in Europe, the most serious endemic diseases of wild aquatic animals have often been traced to the introduction of non-native species (Peeler et al. 2011). Non-indigenous species can transport a variety of organisms, including viruses, bacteria, and other eukaryotes, which are collectively referred to as symbiotes. The risks and impacts of co-transported pathogens and other symbionts remain largely unexplored, unlegislated, and difficult to identify (Foster et al. 2021). Across Europe, dramatic population declines in native species such as crayfish (*Astacus astacus*), oysters (*Ostrea edulis*), and eels (*Anguilla anguilla*) have been linked to diseases introduced with non-indigenous species (Peeler et al. 2011). These severe adverse effects are often due to the lack of immunity in new hosts. The introduction of non-indigenous species in Iceland has increased significantly in the last three decades (e.g. Gunnarsson et al. 2015; Micael et al. 2021, 2022). Therefore, the likelihood of pathogens being transported to Iceland is evident and should be taken seriously to prevent potential ecological and economic impacts.

Suggestions for future monitoring and management

Many management strategies may directly or indirectly influence disease dynamics, particularly if they impact key parameters such as mortality rates, disease transmission, pathogen survival, and host availability (Sokolow et al. 2009). Several priorities have been highlighted in marine disease management (Harvell et al. 2004), including understanding the roles of biotic and abiotic factors in disease transmission, developing predictive models for outbreaks that consider environmental and climatic conditions, and establishing ecosystem-based surveillance programs for emerging marine diseases. Given the expanding fisheries of *C. irroratus* in Iceland

in recent years (Directorate of Fisheries 2025), incorporating empirical data like that presented here is crucial for effectively addressing these management priorities. Integrating such data with spatiotemporal models for disease prevalence, as demonstrated by Tanaka et al. (2017), can serve as a valuable tool for future management decisions. This approach could guide the monitoring and management of crab shell disease, providing policy-relevant insights to enhance ecosystem-based disease surveillance programs, ultimately benefiting the fisheries industry.

Conclusion

In Iceland, the non-indigenous *C. irroratus* has recently been reported to be affected by crustacean shell disease. This is of concern since *C. irroratus* is an exotic species in Iceland and has already been documented to have a negative impact on native species. The high prevalence of shell disease in *C. irroratus* in Iceland could have broader implications for the economy, ecology, and human health and raises significant concerns about the future impact of this invasive species on both native and introduced crustacean populations. Whether the disease was introduced with the crab remains uncertain. Further research and effective management strategies are essential to address this emerging threat and protect the health and sustainability of Icelandic marine ecosystems.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Author contributions

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Author ORCIDs

Sindri Gíslason https://orcid.org/0000-0002-6325-672X
Hermann Dreki Guls https://orcid.org/0000-0002-9862-1053
Joana Micael https://orcid.org/0000-0003-4658-5692
Árni Kristmundsson https://orcid.org/0000-0001-7387-8584
Mark Freeman https://orcid.org/0000-0002-7042-3143
Halldór Pálmar Halldórsson https://orcid.org/0000-0001-5529-1536

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

Authors: Sindri Gíslason, Hermann Dreki Guls, Joana Micael, Árni Kristmundsson, Mark Freeman, Nóa Sólrún Guðjónsdóttir, Halldór Pálmar Halldórsson

Data type: docx

Explanation note: **figure S1**. Proportion of shell disease in *Cancer irroratus* by depth and year. **figure S2.** Boxplot of the maximum number of *Cancer irroratus* per trap by station from 2017 to 2023. The central line in each box indicates the median crab count, while the upper and lower hinges represent the interquartile range. This visualization highlights trends and variability in crab populations across stations over time. **table S1.** Summary of logistic regression models evaluating shell disease prevalence in *Cancer irroratus* in Hvalfjörður, Iceland (2017–2023). Odds ratios (OR) and 95% confidence intervals (CI) are reported for the effect of depth, sex, and carapace width on the likelihood of shell disease. Depth models use 10 m as the reference category; the sex model uses males as the reference. Carapace width was entered as a continuous variable in sex-specific models. **table S2.** Model performance metrics for logistic regression models predicting shell disease prevalence in *Cancer irroratus* (2017–2023). For each model (depth, sex, and carapace width, with the latter analyzed separately by sex), the table reports Akaike Information Criterion (AIC), area under the receiver operating characteristic curve (AUC), McFadden's pseudo-R^2, and Tjur's R^2. These metrics indicate model parsimony, discriminative ability, and explanatory power.

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